

XYLEM ANATOMY OF HIBBERTIA (DILLENiaceae) IN RELATION TO ECOLOGY AND EVOLUTION

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IN A RECENT REVIEW of xylem anatomy, Carlquist (1975) quoted a statement by Bailey (1966), stressing the importance of relating wood anatomical diversity to ecological and physiological influences in habitats where the plants normally grow, and suggested that such relations are best established by comparing species within a genus. A preliminary comparison of this kind is here presented for the genus *Hibbertia* Andr., which contains about 150 species of shrubs, small trees, or vines that occur primarily in Australia and New Caledonia. As pointed out by Stebbins and Hoogland (1976), *Hibbertia* includes an extraordinarily wide range of diversity with respect to growth habit, size and structure of leaves, floral morphology, chromosome numbers, and ecological adaptations. Furthermore, the least specialized members of the genus are in many ways among the least specialized of modern angiosperms with respect to the majority of their morphological characteristics (Stebbins, 1974). The primitive condition of *Hibbertia* xylem in comparison to that of other Dilleniaceae was recognized by Dickison (1967). A thorough analysis of variation in venation patterns of the leaves (Rury & Dickison, 1977) has shown that foliar venation is rather generalized in some species, but highly specialized in others, and that species having relatively specialized floral structures usually have more specialized leaf morphologies. The data reported in this paper can, accordingly, be discussed within the context of the wide morphological and ecological variation present within the genus, and the family Dilleniaceae as a whole.

MATERIALS AND METHODS

Woods of 27 species of *Hibbertia* were studied. Sources of specimens and other pertinent collecting data are presented in TABLE 1. Wood samples were boiled in water and cut on a sledge microtome at a thickness of 20 to 30 μm . Smaller stems were initially glued onto wood blocks prior to sectioning. Resulting sections were stained with safranin. Data relating to wood cell length were obtained by making at least 25 measurements from macerations prepared using Jeffrey's solution. Vessel elements were measured from tip to tip. Cell diameters were measured from transverse sections. Wood terminology follows the *Multilingual Glossary of Terms used in Wood Anatomy* (Committee on Nomenclature, International Association of Wood Anatomists, 1964). For the most part, categories of measurement follow the suggestions of the Committee on Standardization of Terms of Cell Size (1937, 1939).

TABLE 1. Wood specimens of *Hibbertia* examined.

SPECIES	COLLECTOR	COLLECTION LOCALITY	HERBARIUM VOUCHER ^a	XYLARIUM
<i>altigena</i> Schltr.	<i>H. S. MacKee 3549</i>	New Caledonia	L	—
<i>aspera</i> DC.	<i>P. G. Wilson 680</i>	S. Australia	L	—
<i>banksii</i> Benth	<i>L. J. Brass 8431</i>	Papua	L	—
<i>baudouinii</i> Brongn. & Gris	?	New Caledonia	?	BRIw 13033
<i>baudouinii</i> Brongn. & Gris	<i>H. S. MacKee 3818</i>	New Caledonia	L	—
<i>coriacea</i> (Pers.) Baillon	<i>Lam & Meeuse 6068</i>	Madagascar	L	—
<i>cuneiformis</i> (Labill.) Sm.	?	W. Australia	?	BRIw 11684
<i>cuneiformis</i> (Labill.) Sm.	<i>Carlquist 1017</i>	W. Australia	RSA	RSaw
<i>cuneiformis</i> (Labill.) Sm.	<i>Carlquist 6085</i>	W. Australia	RSA	RSaw
<i>drummondii</i> (Turcz.) Gilg	<i>Stebbins & Keighery</i> <i>A-25</i>	W. Australia	UCB	—
<i>exutiacies</i> N. A. Wakefield	<i>Kraehenbuehl 2153</i>	S. Australia	NCU	—
<i>furfuracea</i> (DC.) Benth	<i>Carlquist 6056</i>	W. Australia	RSA	RSaw
<i>glaberrima</i> F. Mueller	<i>D. J. Whibley 1081</i>	S. Australia	NCU	—
<i>huegelii</i> (Endl.) F. Mueller	<i>E. Pritzel 572</i>	Australia	L	—
<i>huegelii</i> (Endl.) F. Mueller	<i>Stebbins & Keighery</i> <i>A-9</i>	Australia	UCB	—
<i>hypericoides</i> (DC.) Benth	<i>A. Morrison s.n.</i>	W. Australia	L	—
<i>lineata</i> Steudel	<i>Carlquist 5940</i>	Australia	RSA	RSaw
<i>lucens</i> Brongn. & Gris	<i>A. C. Smith 3546</i>	Fiji	MAD, NY	SJRw 28402
<i>lucens</i> Brongn. & Gris	<i>A. C. Smith 3045</i>	Fiji	MAD, NY	SJRw 27903
<i>lucens</i> Brongn. & Gris	?	New Caledonia	?	BRIw 12037

TABLE 1. Wood specimens of *Hibbertia* examined (*continued*).

SPECIES	COLLECTOR	COLLECTION LOCALITY	HERBARIUM VOUCHER ^a	XYLARIUM
<i>montana</i> Steudel	<i>Stebbins & Keighery</i> A-38	Australia	UCB	—
<i>ngoyensis</i> Schltr.	<i>H. S. MacKee</i> 32303	New Caledonia	NCU	NCU
<i>obtusifolia</i> DC.	<i>G. L. Stebbins</i> A-53	A.C.T., Australia	UCB	—
<i>obtusifolia</i> DC.	<i>Hoogland</i> 3067	A.C.T., Australia	L	—
<i>potentilliflora</i> Benth	<i>Stebbins & Keighery</i>	W. Australia	UCB	—
<i>procumbens</i> (Labill.) DC.	<i>N. T. Burbidge</i> 3326	Tasmania	L	—
<i>saligna</i> DC.	?	N.S.W., Australia	?	BRIw 13034
<i>saligna</i> DC.	<i>E. F. Constable</i> 4434	N.S.W., Australia	NCU	—
<i>scandens</i> (Willd.) Gilg	<i>R. D. Hoogland</i> 3115	Queensland, Australia	L	—
<i>scandens</i> (Willd.) Gilg	—	Cult. BRI s.n.	—	—
<i>sericea</i> (DC.) Benth	<i>E. F. Constable</i> 3850	N.S.W., Australia	NCU	—
<i>sericea</i> (DC.) Benth	<i>M. C. R. Sharrad</i> 342	S. Australia	L	—
<i>serrata</i> Hotchkiss	<i>C. L. Wilson</i> 855	Australia	US	—
<i>stricta</i> (DC.) F. Mueller	<i>D. J. Whibley</i> 855	S. Australia	NCU	—
<i>trachyphylla</i> Schltr.	?	New Caledonia	L	—
<i>uncinata</i> (Benth) F. Mueller	<i>Stebbins & Keighery</i> A-3	Australia	UCB	—
<i>virgata</i> R. Br. ex DC.	<i>B. J. Blaylock</i> 575	S. Australia	NCU	—

^a Abbreviations follow Holmgren and Keuken (1974) in *Index Herbariorum*.

OBSERVATIONS

GROWTH RINGS. Well-defined growth rings are recognizable by the presence of thicker-walled imperforate tracheary elements in the late wood of the Australian species *Hibbertia drummondii*, *H. huegelii*, *H. montana*, *H. exutiacies*, *H. virgata*, *H. potentilliflora*, *H. saligna*, *H. stricta*, *H. uncinata*, *H. hypericoides*, and *H. obtusifolia*. Very weak growth rings are also evident in *H. cuneiformis* and *H. sericea*. Growth rings are irregularly spaced and conspicuously wavy in outline as viewed in transection. Woods of *H. exutiacies* and *H. virgata* are, in addition, distinctly ring porous, as shown by the restriction of larger vessel elements to the early wood of a growth ring.

VESSEL ELEMENTS. Selected characteristics of the wood of species studied are summarized in TABLE 2. Four species, *Hibbertia lucens*, *H. saligna*, *H. cuneiformis*, and *H. coriacea*, formed the basis of the description of *Hibbertia* wood by Dickison (1967). In spite of the fact that they belong to different sections of the genus (which in floral morphology differ from each other so much that they might best be regarded as subgenera), these species are very similar to each other with respect to xylem structure. Wood of the remaining species is here recorded for the first time and reveals an interesting diversity of anatomical structure previously unreported for the genus *Hibbertia*.

In most plants the shape of the pores varies from slightly angular to circular. In *Hibbertia saligna*, *H. lucens*, *H. cuneiformis*, *H. trachyphylla*, and *H. obtusifolia* the pores are decidedly angular, whereas in *H. scandens*, *H. huegelii*, and *H. exutiacies* there is a strong tendency toward a circular outline. As reported by Dickison (*loc. cit.*), vessel elements are solitary in distribution; the paired condition is present only in the region of vessel element overlap. Walls are typically of medium thickness, but decidedly thin-walled vessels occur in the Australian *H. scandens* and in *H. ngoyensis* of New Caledonia. Vessel walls of the other New Caledonian plants examined also show a tendency toward the thin-walled condition. Mean pore diameters range from extremely small in the low, shrubby species to mostly moderately small in the larger tree forms. In the single collection of *H. hypericoides* studied, pores have extremely small diameters, making it difficult to distinguish vessels from imperforate tracheary elements in transection. Vessel diameter in *H. scandens* has clearly increased in response to the liana habit. The number of pores per unit area varies considerably, being highest in *H. stricta* and *H. exutiacies*, and lowest in *H. scandens*. Within the genus, mean vessel element length ranges between medium sized and moderately long.

Intervessel pitting is sparse, but where present is opposite to transitional to scalariform in distribution. Pits are circular to scalariform in outline and range in size from minute to very large. Ray-vessel pitting is half-bordered with a distribution pattern similar to that of intervessel pitting. *Hibbertia procumbens*, a prostrate semi-xeric species from southeastern

TABLE 2. Summary of selected wood anatomical features of *Hibbertia* in relation to growth habit and habitat.

(Data from immature samples are in parentheses.) The numbers corresponding to character states are: 1, number of samples studied; 2, geographical distribution; 3, ecological preferences; 4, growth habit; 5, leaf size; 6, diameter of stems studied; 7, growth rings; 8, range in vessel element length, $\mu\text{m.}$; 9, mean vessel element length, $\mu\text{m.}$; 10, mean vessel diameter, $\mu\text{m.}$; 11, perforation plates scalariform only; 12, perforation plates scalariform and simple; 13, bars per scalariform perforation, average; 14, mean fiber length, $\mu\text{m.}$; 15, fiber wall thickness.

Section and species	1	2	3 ^a	4	5 ^b	6 ^c	7 ^d	8	9	10	11	12	13	14	15 ^e
Polystiche															
<i>baudouinii</i>	2	New Caledonia	M	rosette tree, 10 m.	L. S. 4	M	-	660-1408	1078	57	+		17	1441	m, t
Spicatae															
<i>ngoyensis</i>	1	New Caledonia	M	rosette tree, 6 m.	L. S. 3	M	-	759-1243	968	95	+		22	1804	t
<i>lucens</i>	3	New Caledonia, Fiji	SX	shrub or rosette tree	L. S. 3	M	-	625-2037	1074	61	+		42	1551	m, t
<i>trachyphylla</i>	1	New Caledonia	SX	shrub or rosette tree	L. S. 3	6.0 mm.	-	(418-1034)	(726)	(40)	+		(24)	(1056)	m, t
<i>altigena</i>	1	New Caledonia	SX	shrub, 1.0 m.	L. S. 2	4.0 mm.	±	(341-1012)	(682)	(35)	+		(32)	(1001)	m
Cyclandra															
<i>saligna</i>	2	E. Australia, N.S.W.	M	erect shrub, 60-90 cm.	L. S. 3	M	+	770-1694	1199	38	+		46	1351	m, t
<i>serrata</i>	1	S.W. Australia	M	shrub, 2-3 m.	L. S. 3	? ^f	?	?	979	?	+		32	1133	?
<i>obtusifolia</i>	2	S.E. Australia	SX	small, erect shrub, 0.1 m.	L. S. 3	4.0 mm.	+	308-957	627	25	+		17	825	m
<i>scandens</i>	2	E. Australia	M	vine	L. S. 3	8 mm.	-	413-1430	731	45	+		9	943	t

<u>montana</u>	1	W. Australia	SX	shrub, 0.5-1.5 m.	L. S. 2	2.0 mm.	+	440-990	651	14	+	8	747	m
<u>drummondii</u>	1	Interior of W. Australia	X	shrub, 0.5 m.	L. S. 2	2.5 mm.	+	220-880	513	13		+	2	803 th
<u>glaberrima</u>	1	Interior of S. & N. Australia	SX-X	shrub	L. S. 2- L. S. 3	4.0 mm.	-	220-825	497	23		+	3	760 m, th
<u>potentilliflora</u>	1	W. Australia	SX	semi-prostrate shrub	L. S. 3	4.1 mm.	+	270-622	411	15	+		4	551 m
<u>virgata</u>	1	E. Australia	SX	shrub, 0.5 m.	L. S. 1	3.5 mm.	+	248-550	400	14	+		8	584 m, t
<u>procumbens</u>	1	Tasmania, E. Australia	SX	prostrate shrub	L. S. 1- L. S. 2	-	?	165-671	451	?	+		28	517 ?
Candollea														
<u>cuneiformis</u>	3	S.W. Australia	SX-M	shrub, 1-2 m.	L. S. 2- L. S. 3	M	±	572-1232	940	39	+		24	1402 m, t
<u>huegelii</u>	2	W. Australia	SX	shrub, 0.5 m.	L. S. 2	4.0 mm.	+	330-1265	573	13	+		8	738 m, th
<u>uncinata</u>	1	Interior of W. Australia	X	shrub, 0.2-0.5 m.	L. S. 1	3.0 mm.	+	330-853	547	13		+	4	767 m, th
Hemipleurandra														
<u>lineata</u>	1	W. Australia	SX	semi-prostrate shrub	L. S. 3 (?)	-		473-869	627	30	+		7	957 ?
<u>furfuracea</u>	1	S.W. Australia	SX	shrub, 0.5-1.5 m.	L. S. 3	-		528-979	726	40	+		10	935 ?
<u>hypericoides</u>	1	S.W. Australia	SX-M	shrub	L. S. 2	4.5 mm.	+	363-1056	616	20	+		7	792 m, t
Pleurandra														
<u>sericea</u>	2	E. Australia	SX	shrub, 0.5-1 m.	L. S. 2	3.3 mm.	+	363-1265	697	22	+		9	998 m, th
<u>stricta</u>	1	E. & S. Australia	SX	shrub, 0.5 m.	L. S. 1	3.2 mm.	+	193-770	481	17	+		8	759 m

1978]

DICKISON ET AL., HIBBERTIA

TABLE 2. Summary of selected wood anatomical features of Hibbertia in relation to growth habit and habitat (continued).

<u>exutiacies</u>	1	S.E. Australia	SX	prostrate shrub	L. S. 1	3.8 mm.	+	231-660	430	21	+	5	613	m
<u>aspera</u>	1	S.E. & W. Australia	SX	shrub	L. S. 2	3 mm.		352-792	561	?	+	7	770	?
Hemistemma														
<u>coriacea</u>	1	Madagascar	SX	shrub, 0.6-2 m.	L. S. 2- L. S. 3	M	-	693-1287	957	40	+	19	1474	m, t
<u>banksii</u>	1	N. Queensland, Australia; S. New Guinea	M	shrub, 1-2 m.	L. S. 3	-		671-1430	968	?	+	12	1144	?

^aSymbols used: mesic (M), semi-xeric (SX), or xeric (X).

^bLeaf size classes after Raunkiaer (1934): (L. S. 1) Leptophylls 0-25 mm.²; (L. S. 2) Nanophylls 25-225 mm.²; (L. S. 3) Microphylls 225-2025 mm.²; (L. S. 4) Mesophylls 2,025-18,222 m².

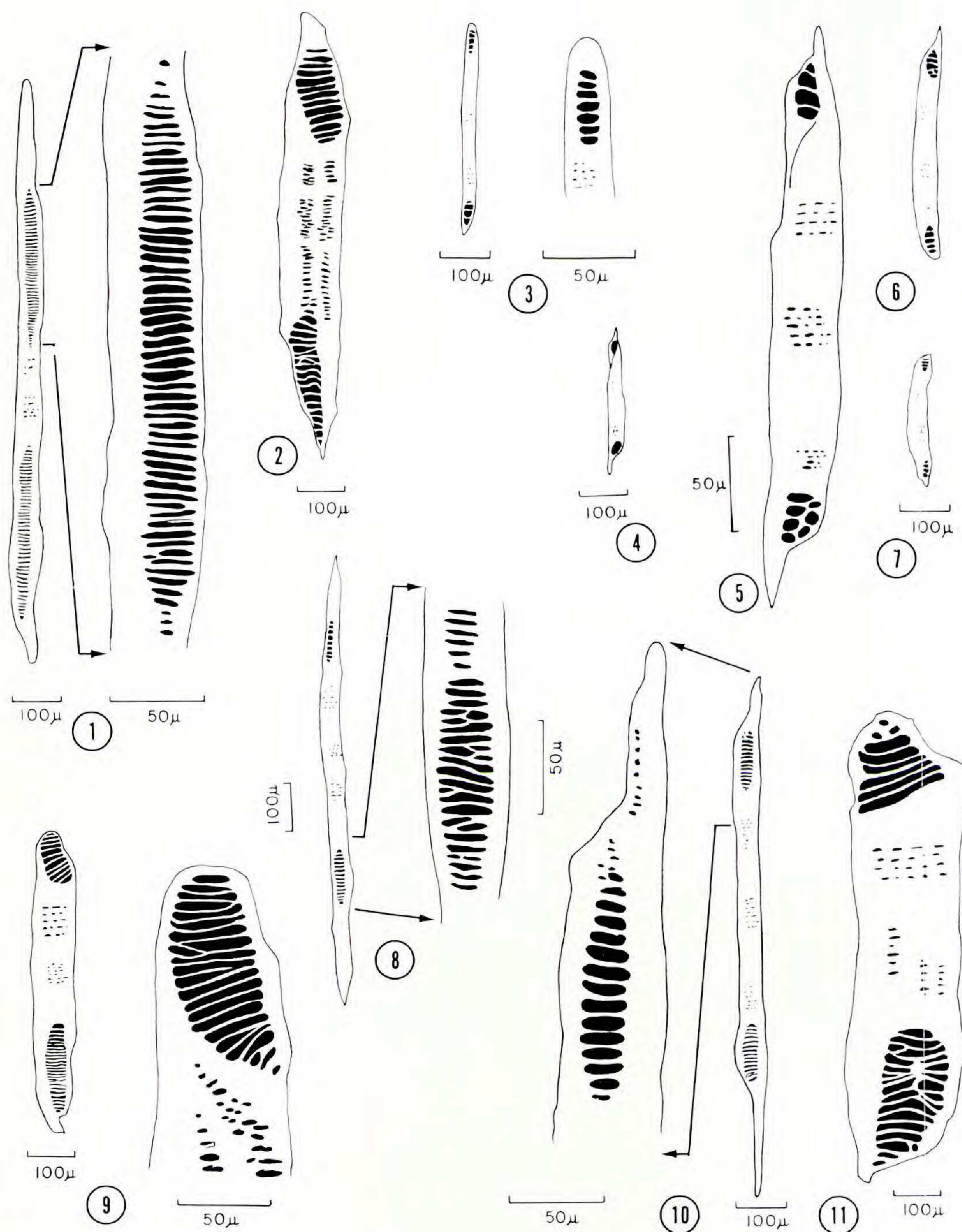
^cSymbol used: mature wood (M).

^dSymbols used: growth rings present (+), or absent (-).

^eSymbols used: walls thin - lumen greater than thickness of walls (t); medium - lumen equal to thickness of walls (m); or thick - lumen less than thickness of walls (th).

^fSymbol used: data unavailable (?).

Australia, is unusual in possessing extensive scalariform lateral wall pitting. Perforation plates are exclusively scalariform in the vast majority of species, although there is wide variation in the number of bars per perforation. In our material mean bar number ranges between a high of 42 and a low of 2 (FIGURES 1-10). Bars also vary considerably in width and degree of separation. Branched bars are frequent. It is of much interest



FIGURES 1-11. Vessel member structure in *Hibbertia* and *Pachynema*: 1, *Hibbertia saligna* (BRIw 13034); 2, *H. baudouinii* (BRIw 13033); 3, *H. sericea* (Sharrad 342); 4, 5, *H. uncinata* (Stebbins & Keighery A-3); 6, 7, *H. exutiacies* (Kraehenbuehl 2153); 8, *H. obtusifolia* (Stebbins A-53); 9, *H. cuneiformis* (BRIw 11684); 10, *H. banksii* (Brass 8431); 11, *Pachynema junceum* (Dunlop s.n.).

that simple perforation plates were observed in a low percentage of the vessel elements in *H. drummondii*, *H. glaberrima*, and *H. uncinata* (FIGURE 4). In these species vessel elements are occasionally present with simple perforations on one end and few-barred scalariform perforation plates on the other.

IMPERFORATE TRACHEARY ELEMENTS. Imperforate tracheary elements are fiber-tracheids, although in many of the small, semi-xeric species the pit borders are very reduced, and the elements approach the libriform fiber type. The mean length of the fiber tracheids generally ranges within the very short and short categories; only *Hibbertia lucens* and *H. ngoyensis* have imperforate tracheary elements that can be classified as long. Bordered pits are usually present on both radial and tangential walls and have minute to large diameters. In the New Caledonian species the pitting is often distributed in multiseriate rows. The walls of fiber tracheids vary considerably in thickness. Thin-walled elements (cell lumen greater than thickness of walls) occur in *H. scandens*, *H. baudouinii*, *H. lucens*, *H. trachyphylla*, *H. saligna*, *H. virgata*, *H. cuneiformis*, *H. hypericoides*, *H. coriacea*, and particularly *H. ngoyensis*. Thick-walled elements (cell lumen almost completely closed) characterize *H. glaberrima*, *H. huegelii*, *H. uncinata*, *H. sericea*, and particularly *H. drummondii*.

RAYs. Rays are heterogeneous, and in plants with abundant xylem both multiseriate and uniseriate rays are present. In Australian plants with limited secondary xylem production, generally only uniseriate rays occur, although these may occasionally become biseriate. Multiseriate rays are present in New Caledonian species in the first-formed secondary xylem. Multiseriate rays are 1 to 5, mostly 1 to 3, cells wide, are composed primarily of upright cells, and have long uniseriate wing extensions of the upright cells. Rays tend to be numerous to abundant per square mm.

AXIAL PARENCHYMA. Axial parenchyma is diffuse and scanty in distribution, although it becomes increasingly scarce in more xeric species. Axial parenchyma is rare in plants like *Hibbertia drummondii*. Numerous raphides are present in enlarged axial parenchyma cells of *H. cuneiformis* and *H. virgata*.

DISCUSSION

In the genus *Hibbertia*, trends of specialization with respect to growth habit have been chiefly toward small, thin-stemmed, prostrate or semi-prostrate shrubs; and with respect to leaves primarily toward leptophylls and nanophylls (*sensu* Raunkiaer, 1934) having various kinds of specializations associated with drought resistance. Nodal anatomy has frequently been reduced from the trilacunar to the unilacunar pattern. The resulting diversity in plant habit, and, therefore, the amount of secondary xylem produced, makes an evaluation of the wood anatomical data obtained from this genus difficult. The dangers in comparing data from woods of different

ages and growth habits are well known. Nevertheless, it is clear that *Hibbertia* has undergone an extensive adaptive radiation that has often resulted in reduced plant size in response to increasingly arid conditions. The combination of decreased plant stature and decreased water availability has produced significant alterations in xylem structure.

Hibbertia species from mesic habitats show an absence of growth rings. Seasonality of climate is reflected in xylem with growth rings and even ring porosity. In *Hibbertia*, vessel elements have frequently become shorter, a trend noted for other xeric taxa by Carlquist (1975), and their perforation plates have acquired a reduced number of bars (less than 10) with a few species even possessing occasional simple perforation plates. Small differences in vessel member length are not here regarded as important, although variation representing different size classes of elements is significant. In dicotyledons as a whole, these trends have usually been accompanied by an increase rather than a decrease in pore diameter. In *Hibbertia* a reduction in vessel element length is associated with a reduction in pore width. These tendencies are also combined with an increase in pore number per unit area. It must be kept in mind, however, that there has also occurred a dramatic decrease in the total amount of xylem produced in the xeric plants. The only exception in the trend toward smaller pore diameters in small-stemmed species is *H. scandens*, a liana, in which vessels are very wide in comparison with stem diameter, yet have retained scalariform perforation plates with a moderate bar number.

With regard to correlations between perforation plate type and ecological factors, van der Graaff and Baas (1974) and Carlquist (1975) presented evidence to show that no general trend can be established in dicotyledons as a whole, an opinion further enunciated and documented by Baas (1976). Individual genera, however, occasionally do show such correlations. *Hibbertia*, for example, demonstrates a high degree of correlation between mesic habitats and longer vessel elements with many-barred scalariform perforation plates, and xeric habitats and vessel elements with reduced length, diameter, and bar number in scalariform perforations. The only notable exception is the xeric species *H. procumbens*, which has short, narrow vessel elements, yet has retained scalariform perforation plates with a high number of bars. The scalariform lateral wall pitting on the vessel elements of this species is also unusual. It is very clear that in *Hibbertia*, habit-related anatomical modification is superimposed upon evolutionary, habit-related, and/or physiological specialization, and the separation of these facets is difficult.

Four other families of angiospermous shrubs occur regularly in association with the specialized Australian species of *Hibbertia*: Proteaceae, Leguminosae (especially *Acacia*), Myrtaceae, and Epacridaceae. In the first three families, vessel elements are short, comparatively wide, and have simple perforations. The Epacridaceae, however, resemble *Hibbertia* in that several species have vessel elements with small or very small diameters and scalariform perforation plates. The Proteaceae, Leguminosae, and Myrtaceae contain large shrubs and trees, and most of the recorded data

are from these larger species. The Epacridaceae, on the other hand, contain chiefly small, slender-stemmed shrubs similar in growth habit to *Hibbertia*. Baas (1976) has observed that in the Epacridaceae, the genera with scalariform plates show a mesic preference, and the genera with exclusively or predominantly simple plates prefer xeric habitats.

RELATION BETWEEN WOOD ANATOMY AND TAXONOMY. As reported by Stebbins and Hoogland (1976), the genus *Hibbertia* is remarkable for its great range of variation with respect to leaf size, shape, and structure, as well as to floral morphology. The present study reveals an additional large range of variation with respect to secondary xylem structure, particularly in vessel element morphology. In many of the principal sectional groups (*sensu* Gilg & Werdermann, 1925), which differ from each other with respect to floral morphology, the trend toward medium-sized to small, often acicular leaves can be found as an independent course of evolution (Rury & Dickison, 1977).

Within each section or sectional group (considering HEMIPLEURANDRA, HEMISTEMMA, and PLEURANDRA as a single group) there appear to be parallel trends of specialization. In leaf morphology they consist of reduction in leaf size and venation, and increase in the proportion of sclerenchymatous tissue; in floral morphology there has been reduction in size and number of parts; and in vessel elements, reduction in length, diameter, and number of scalariform perforation plate bars, all correlated with an overall reduction in plant size. A different combination is seen in *Hibbertia scandens* (section CYCLANDRA, subsection SUBSESSILES), in which larger leaves and flowers are associated with vessel elements showing no reduction in diameter. This species has also become specialized differently in growth habit, since it is a vine rather than a small shrub. The three New Caledonian sections exhibit considerable homogeneity in their wood anatomy. In addition, they have many similarities to section HEMISTEMMA, a relatively mesophytic species group from northern Australia, New Guinea, and Madagascar. A very interesting parallelism in leaf and nodal structure also occurs within these sections separated by floral characters. The New Caledonian subsection TRIMORPHANDRA, placed by Gilg and Werdermann (1925) within the highly heterogeneous Australian section CYCLANDRA on the basis of floral morphology, exhibits a leaf morphology identical to that of the New Caledonian hibbertias (Rury & Dickison, 1977). Although wood specimens of subsection TRIMORPHANDRA were not available for study, we strongly suspect that the wood anatomy of these species would serve to support the suggested transferral of this subsection to one of the New Caledonian sections of *Hibbertia*.

A lack of correlation is evident when *Hibbertia* is compared with two of its nearest relatives, *Didesmandra* and *Schumacheria*. These genera have longer vessel elements with larger numbers of scalariform perforation plate bars than any species of *Hibbertia* (Dickison, 1967). Nevertheless, their flowers are bilaterally symmetrical, and in the reduction of the ovules to one per carpel, as well as in floral anatomy, they are more special-

ized than any species of *Hibbertia* (Dickison, 1968; Wilson, 1973). *Pachynema*, the third genus related to *Hibbertia*, is essentially leafless and has a much reduced floral structure (Wilson, 1973). Examination of the secondary xylem of *P. junceum* (*van Steenis 17664* and *C. Dunlop s.n.*) reveals that vessel elements are medium sized in length (242–627 μm ., mean 440 μm .) with scalariform perforation plates. The number of bars per scalariform perforation plate ranges from 2 to 15 with an average number of 7 (FIGURE 11). Fiber-tracheids are very short in length (363–902 μm ., mean 660 μm .).

RELATION BETWEEN VESSEL ELEMENT STRUCTURE AND GEOGRAPHIC DISTRIBUTION. The species having the least specialized vessel elements include endemics to each of the major geographic regions where *Hibbertia* occurs (eastern Australia, southwestern Australia, New Caledonia, Madagascar) with the exception of northern Australia, from which no specimens have yet been examined. However, since the species of northern Australia resemble *H. coriacea* of Madagascar and *H. lucens* of New Caledonia in most characteristics, and occur in similar habitats, there is good reason to believe that most of them have relatively unspecialized vessel members. With the exception of *H. scandens*, which occurs from southeastern Australia northward to New Guinea, all of the species known to have more specialized vessel elements occur in southeastern, southwestern, or interior Australia, and inhabit temperate or subtropical rather than tropical regions. Trends toward leptophylly with accompanying reduction in length and diameter of vessel elements occur in species endemic to southeastern Australia (*H. virgata*), to the dry interior (*H. glaberrima*), and to southwestern Australia (*H. huegelii*), as well as in species groups that are distributed all across the continent (*H. stricta*). The three species observed to possess occasional simple perforation plates are all from the interior region of Australia. The evidence from geography, therefore, supports that from floral morphology to indicate that in various parts of temperate Australia, independent trends toward xylem specialization have occurred contemporaneously. Although in *Hibbertia* reduction in vessel member length and diameter is apparently the result of a multitude of biotic and abiotic factors, these trends do follow the general trends for other dicotyledons of decreased vessel element length and diameter with increasing latitude (van der Graaff & Baas, 1974).

RELATION BETWEEN WOOD STRUCTURE AND HABITAT. The trends of specialization of vessel elements toward shortening, reduction in diameter, reduction in the number of bars on scalariform perforation plates, and even the formation of simple plates, that are reported for the genus *Hibbertia* are clearly associated with occupation of drier habitats, including those like the heathlands of eastern Australia. Similar trends are reviewed by Carlquist (1975) for desert shrubs and high montane or alpine cushion plants belonging to various families. Associated with these changes in *Hibbertia* vessel structure, is a concomitant decrease in length and in-

crease in wall thickness of imperforate tracheary elements and an overall decrease in the amount of axial parenchyma. The species with the thickest fiber-tracheid walls is *H. drummondii*, a species also characterized by the occasional occurrence of simple perforation plates, which grows in the dry Australian interior.

Nevertheless, a different picture emerges when one compares the least specialized species belonging to each of the sections with each other, and also when *Hibbertia* is compared with other genera of Dilleniaceae. These species, although by no means xerophytic, do not always occupy the wetter habitats of the regions where they are found. *Hibbertia saligna*, a species with comparatively primitive vessel members, is generally distributed on ridge crests and mountainsides in a forest of *Eucalyptus* spp. This species of *Hibbertia*, because of the tendency of *Eucalyptus* leaves to hang vertically, receives abundant light on the forest floor. *Hibbertia serrata*, *H. cuneiformis*, and *H. lucens* are three additional species which possess vessel elements having scalariform perforation plates with 24 to 42 bars. The first two of these species grow in southwestern Australia where annual precipitation is ample, from 40 to 60 inches, but where the summer drought lasts from four to five months. In this region, they occur in relatively dry as well as more mesic sites. *Hibbertia lucens* has a tropical habitat, but according to herbarium labels it grows in dry, open forests rather than in wet rain forests. All of the New Caledonian species that were investigated have comparatively primitive vessel members. *Hibbertia baudouinii* occurs in more mesic situations than does *H. lucens*, and the specimen of *H. ngoyensis* studied grew in a humid forest. The remaining species having vessel elements with 20 or more bars per scalariform perforation plate are *H. coriacea* of Madagascar, which grows in the climatically moist eastern side of the island (but according to herbarium labels in dry, sunny places or on sandy soil that is subject to periodic drought), and *H. obtusifolia*, the specimen of which was collected in a dry *Eucalyptus* forest near Canberra, Australia. Fiber-tracheid walls of these plants tend to be thinner than in other species. Also, all of the above species of Madagascar and New Caledonia have a more regular, better-developed system of both low and high order venation.

Present evidence suggests, therefore, that the correlation between vessel element specialization and adaptation to drought holds well for trends within the Australian species of *Hibbertia*, but that the situation within the genus as a whole, particularly among the species of northern Australia, New Caledonia, and Madagascar, is less clear. Any conclusions about these species must await the study of additional material.

The same ambiguity arises when other genera of Dilleniaceae are examined. Long vessel members having exclusively scalariform perforation plates with many bars occur in *Dillenia*, *Schumacheria*, and *Didesmandra*. Whereas the latter two genera are rain forest plants, *Dillenia* grows in a variety of habitats including lowland rainforests, savannas, and monsoon forests with pronounced dry periods (Baas, 1976). Another dilleniaceous genus with scalariform perforation plates is *Acrotrema*, a woody herb that

grows in wet areas. These genera, however, are distinctly more specialized with respect to floral morphology than is *Hibbertia* (Dickison, 1968; Wilson, 1973), so they cannot be regarded as being more (or even as) closely related to the common ancestor of the Dilleniaceae than is *Hibbertia*. The presence in *Pachynema complanatum* of elongate vessel elements of which the scalariform perforation plates have 16 to 48 bars (Dickison, 1967) is truly remarkable, and a re-examination of this species with new material would be highly desirable. This species grows in the tropical monsoon climate of northern Australia where it is subjected to five months of winter drought. It is a shrublet bearing leafless, flattened stems and much-reduced flowers. The habit of the plant, and even more that of other species of *Pachynema*, such as *P. junceum*, suggests a long history of adaptation to aridity. The occurrence of scalariform elements in *Pachynema* suggests the possibility of an early derivation of this genus from the ancestral hibbertias and a subsequent radiation into xeric habitats, rather than a more recent derivation from the extreme xeromorphic forms of *Hibbertia*. Consequently, the anatomy and the ecological preferences of the least specialized species of Dilleniaceae do not support the hypothesis that their ancestor evolved in a tropical rain forest climate, and that specialization has been continuously and irreversibly associated with adaptation to greater aridity.

WOOD ANATOMY AND LEAF MORPHOLOGY IN RELATION TO HABITAT. Vegetative character syndromes observed in the growth habit, nodes, and leaves of numerous species of *Hibbertia* represent the evolutionary products of morphological adaptation within diverse ecological situations (Rury & Dickison, 1977). The present study reveals ecologically adaptive character syndromes in the wood anatomy of *Hibbertia* which are clearly correlated with both habit and habitat of the species studied (TABLE 3). It appears that the vegetative and wood anatomical character syndromes of these hibbertias have evolved, in general, as a single vegetative unit in response to environmental selection (TABLES 3, 4). Hence the wood anatomy, nodal structure, and leaf morphology and venation are best regarded as a "morphological continuum" which has evolved as a unit during the ancient adaptive radiation of this genus (*sensu* Stebbins, 1974).

The Australian hibbertias exhibit a heterogeneous species assemblage with respect to leaf size, leaf morphology, and floral structure. The most mesic species of Australia occur as small (*Hibbertia saligna*) to large (*H. serrata*) shrubs, or rarely vines (*H. scandens*, *H. dentata*). In these plants, features such as long, wide, scalariform vessel elements with numerous bars, and thin-walled fibers are correlated with mesomorphic leaves with primitive (*sensu* Hickey & Wolfe, 1975) leaf venation patterns. All mesophytic species examined, with the exception of *H. hypericoides*, possess three-trace, trilacunar nodes, a feature considered as primitive for *Hibbertia* and the entire family Dilleniaceae (Dickison, 1969). The presence of such features as short vessels with few bars (mean 7) per perforation plate, unilacunar nodes, reduced leaves (nanophylls), and reduced leaf venation in *H. hy-*

TABLE 3. Wood anatomical features and leaf sizes of 27 species of *Hibbertia* in relation to habitat type and geography.

SPECIES GROUPING	LEAF SIZE CLASS ^a	VESSEL ELEMENT LENGTH, μ m.	PORE DIAMETER, μ m.	NO. BARS PER PLATE	FIBER LENGTH, μ m.	FIBER WALL THICKNESS ^c
Australian mesic						
(8 spp.) mean	L. S. 3	851	30	21	1059	m-t
range	L. S. 2, 3	308-1694	14-45	6-80	792-1402	
New Caledonian mesic						
(2 spp.) mean	L. S. 3	1023	76	20	1623	m-t
range	L. S. 3, 4	968-1078	57-95	17-22	1441-1804	
Total mesic species						
(10 spp.) mean	L. S. 3	885	42	21	1172	m-t
range	L. S. 2-4	308-1694	14-95	6-80	792-1804	
Australian semi-xeric						
(11 spp.) mean	L. S. 2	585	22	10	801	m
range	L. S. 1-3	165-1265	14-40	0-37	517-1402	t-th
Island semi-xeric ^b						
(4 spp.) mean	L. S. 3	863	45	29	1188	m-t
range	L. S. 2, 3	341-2037	35-61	13-50	1001-1551	
Total semi-xeric species						
(15 spp.) mean	L. S. 2	655	28	15	898	m
range	L. S. 1-3	165-2037	13-61	0-50	517-1551	t-th
Xeric species (Australian)						
(2 spp.) mean	L. S. 2	522	18	3.5	764	m-th
range	L. S. 1-3	497-547	13-23	3-4	760-767	

^a Leaf size classes: see TABLE 2.
^b Fiji, New Caledonia, and Madagascar.
^c Fiber wall thicknesses: t, thin; m, medium; th, thick.

TABLE 4. Wood anatomical features of 27 species of *Hibbertia* in relation to their leaf size classes.

LEAF SIZE CLASSES ^a	VESSEL ELEMENT LENGTH, μ m.	PORE DIAMETER, μ m.	NO. BARS PER PLATE	FIBER LENGTH, μ m.	FIBER WALL THICKNESS ^c
L. S. 1, 2 (12 spp.) mean	559	19	11	757	m
L. S. 2, 3 ^b (4 spp.) mean	726	28	12	1017	m
L. S. 3, 4 (11 spp.) mean	897	45	23	1206	m-t

^a Leaf size classes: see TABLE 2.
^b Excluding species with exclusively L. S. 2 or L. S. 3 leaves, i.e., leaves of intermediate sizes.
^c Fiber wall thicknesses: t, thin; m, medium; th, thick.

pericoides, a species of semi-xeric and mesic habitats, suggests that this species may be a secondary radiant into mesic areas.

All of the mesophytic island species of *Hibbertia* exhibit a vegetative morphological strategy which differs from that of the mesophytic Australian *hibbertias*. The large shrubs and rosette trees of these island habitats possess trilacunar nodes and large, entire leaves with strong intramarginal veins and a very rigid, regular, and well-developed system of low (brochidodromous) and high order venation. These mesophytes, however, possess long, scalariform vessel elements which, with the exception of a slightly larger pore diameter, are very similar to those of their shrubby Australian counterparts. The non-expandible, tear-resistant leaves of these island *hibbertias* thus appear to represent the result of evolution within a relatively non-seasonal, growth-promoting habitat where the potential for sudden leaf expansion in response to ephemerally favorable microclimatic conditions would not be advantageous. The occurrence of such mesomorphically advanced leaf venation patterns in plants with relatively primitive wood anatomy represents a type of mosaic evolution which is also evident in other genera of Dilleniaceae.

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